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CLIMATIC CONSTRAINTS AND ISSUES OF SCALE CONTROLLING REGIONAL BIOMES

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ABSTRACT

The prospect of climatic change threatens to cause large changes in regional biomes. These effects could be in the form of qualitative changes within biomes, as well as spatial changes in the boundaries of biomes. The boundaries, or ecotones, between biomes have been suggested as potentially sensitive areas to climatic change and therefore useful for monitoring change. Regional gradients of vegetation habitat size and variability are explored for their utility in detecting ecotone location and movement as driven by climatic change. Maximal habitat variability, as indicated by differential survivorship of plants, occurs at the ecotones or transitions between biomes. The principles developed for the analysis of abrupt changes in spatial habitat patterns (ecotones) will also be considered for the analysis and detection of potentially abrupt physiognomic changes through time (thresholds) over large regions. Extensive regional changes in habitat variability could occur rapidly, indicating an impending 'ecotone' in time (threshold) over much of the region. Rapid, regional changes could produce significant negative impacts on biological diversity. The two types of change, boundary shifts of regions and physiognomic shifts within regions, are potentially independent and may require different monitoring strategies to detect impending change.

Keywords: biodiversity, biogeography, biomes, climate change, ecotones, landscape variability.

INTRODUCTION

The prospect of rapid, human-caused global change has awakened a need for large-scale ecological science. The task of adapting to or mitigating the potential change could be enormous. Research needs should be prioritized, to identify sensitive regions and ecosystems and to define cost-effective management practices. Ecotones might be sensitive early warning systems of regional change, as well as being important systems in their own right (di Castri et al. 1988). They are, for example, being valued as landscape corridors for the migration of organisms, as barriers to (or facilitators of) flows of energy and matter across them, and as habitats of high biological diversity, among others (Ibid.).

The potential responses of biomes (the major vegetation types of Earth) to climatic change are the focus of this paper. The ecotones between forest and grassland, for example, could rapidly shift across the landscape. Such boundaries are readily observable from satellites and might, therefore, comprise an obvious monitoring tool for the impacts of climatic change. On the ground, however, direct observation of ecotones is less obvious. A theory will be developed in this paper relating regional climatic gradients to regional patterns of habitat variability and the utility of these patterns in 1) locating ecotones on the ground, 2) detecting change in these ecotones through space, and 3) the implications of these patterns of habitat variability to regional and local patterns of biodiversity of plants. The concepts developed from the analysis of spatial habitat variability will then be examined for their potential application to the variation of habitat patterns through time.

Changes in the ecological characteristics of entire biomes could accompany ecotone movement through space. Ecotone is a term usually reserved for abrupt spatial change in ecological communities. However, abrupt change through time over large regional extents, appears quite possible without necessarily affecting the boundaries of the region (Neilson 1986, Neilson et al. 1989). Forested regions, for example, could convert to savanna. How might we anticipate potential physiognomic changes of biomes and would they happen slowly or rapidly? Can we use patterns of spatial habitat variability and the changes in that variability over time as an early warning of potential threshold changes in the structure and function of regional biomes? The term 'threshold' will be used interchangeably with 'ecotone in space', but applies to the more general concept of abrupt change in either space or time.

The general approach will be to examine the scale of habitat patch size as 'perceived' by the organism. That is, a habitable patch for a tree could be restricted to the size of a north-facing slope, or it could encompass both north and south-facing slopes over a larger landscape. A change in the size of a suitable habitat patch will be referred to as a re-scaling of habitat size relative to a particular organism. Regional gradients in the scaling of physical habitat variability by organisms will be examined with regard to ecotones and regional climatic gradients.

The regional patterns of habitat scale (size) and variability (diversity), through space and time, will be explored as a potential indicator of proximity to ecotones or to regional ecosystem thresholds through time. Habitat diversity has long been recognized as a contributor to patterns of species diversity, different habitats fundamentally favoring different species (Cody 1975, MacArthur 1972). Habitat diversity should be assessed relative to the species of interest. For example, experimentally

observed survivorship, growth and reproduction of a single species across nested gradients of physical habitats constitutes a bioassay and will reveal the 'realized' habitat variability as 'perceived' by the organism (Neilson and Wullstein 1983). If seedlings of a given species survive equally well on a range of qualitatively different microhabitats, the range of microhabitats is 'perceived' as homogeneous and the size of the habitat is large. The habitat will also be constrained to ecologically similar species. However, if the seedlings exhibit differential survivorship across a range of qualitatively different microhabitats, then some of the sites will be better suited to ecologically different species, thus promoting a regional increase in species diversity (Axelrod 1967, Neilson and Wullstein 1983, Stebbins 1952). The more habitats as 'perceived' by a single species, the richer should be the community composition.

SCALING OF HABITAT PATTERNS

Habitat pattern at the coarse scale is one of relatively homogeneous biomes separated by ecotones of varying abruptness. The distribution of biotic communities at the biome scale is primarily determined by climate with a secondary influence from soils (Whittaker 1975). That is, the climate determines if a region will support a forest or a grassland, while the soil influences local patterns of composition, health, and density. Therefore, physiognomic diversity should be predictable from environmental factors; while, prediction of species diversity will require the capability to predict physiognomy plus knowledge of biotic interactions and evolutionary and migratory history (Mooney 1977).

Diversity is usually considered to have two components, richness and evenness. Species richness is the number of different species, while evenness reflects their relative abundance (Pielou 1975). For simplicity, subsequent discussion will be restricted to species richness. Alpha diversity is defined as local diversity or species packing, typically that species richness measured in a small plot (Cody 1975, Whittaker 1972). Gamma diversity refers to the diversity of some arbitrarily large region, typically measured as total species richness among a number of small plots throughout a region (Ibid.). Beta diversity is the rate of change of species composition along a gradient and is usually measured by applying a similarity index to adjacent plots along a transect (Ibid.). At the continental or biome scale, species diversity patterns would be considered as gamma diversity and are often illustrated in contour maps of total species number over large geographic space (e.g. Cody 1975, Currie and Paquin 1987, Simpson 1964).

Delcourt and Delcourt (1990) demonstrated that beta diversity at the biome scale is relatively low in core areas and increases to a maximum at

biome ecotones. They analyzed gradients of beta diversity across biomes, intersecting both core and ecotonal areas, and by constructing transects through time, examining periods of stasis and change. The temporal approach of examining stasis and change in species composition is analogous to the spatial analysis of core and ecotonal areas. In both cases the emphasis is placed on the rate of change of species composition along some gradient, either time or space. Beta diversity was shown to peak at ecotones in space and at rapid transition points, or thresholds of physiognomic change, in time (Ibid.).

I propose that the primary process controlling both the spatial and temporal gradients in beta diversity is the climatic constraint on the scaling of habitat space as 'perceived' by the organism. Regional climatic gradients produce regional gradients in habitat scale and diversity with minimum size and maximum diversity occurring at ecotones and at rapid climatic transitions in time (Delcourt and Delcourt 1990). If the spatial and temporal gradients in beta diversity can be causally related to common gradients of habitat structure, we may be able to monitor the spatial and temporal patterns of habitat scale as an early warning signal of climatic change. One such relationship was demonstrated with a regional bioassay of microhabitat suitability along spatial and temporal climatic gradients (Neilson and Wullstein 1983).

ECOTONES IN SPACE - REGIONAL BIOMES

A plot (Fig. 1) of the different global biomes on a state-space of mean annual temperature and mean annual rainfall (Whittaker 1975) indicates that the biomes occupy broadly unique regions of the state-space'. There are two types of transitions in the diagram. First, there are large areas in the plot, particularly the semi-arid grassland region, where the biome could be one of a number of states from grassland to woodland depending on other conditions, such as seasonality or interannual variability of weather or human influence (Neilson 1986, Neilson 1987a, Whittaker 1975). The second type of transition (Fig. 1) is represented by the lines separating different biome types. These lines should also be considered as somewhat 'fuzzy,' in that constraints of climate seasonality and other factors, such as presence and intensity of grazing or fire, will produce physiognomic shifts in one direction or another (Ibid.). The seasonality and year-to-year variability of weather, as well as various disturbance regimes, should modulate the

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'The Holdridge life-zone approach is a more complicated, but fundamentally similar, approach to that of Whittaker (Brown and Gibson 1983). For the sake of simplicity, I will restrict this discussion to the Whittaker approach.

expressed state of the system within the constraints of annual temperature and rainfall (Allen and Starr 1982, Neilson 1986, O'Neill et al. 1986).

The Whittaker state-space diagram (Fig. 1) contains no spatial or temporal dimensions. The transition zones in the state-space diagram could represent rapid physiognomic transitions in space (ecotones) with a minor change in climate, or could imply a rapid physiognomic change in time over entire regions with a minor change in climate. The concepts presented in the diagram are equally valid in both dimensions of time or space. I will first discuss the spatial implications and then generalize to the temporal dimension. Also, by relating weather variability to the timing of plant life-history states and their seasonal physiological characteristics, mechanistic hypotheses relating climate to biome physiognomy can be constructed.

The spatial patterns of seasonal weather associated with the different biotic regions of the conterminous U.S. were analyzed by constructing a grid of line transects over the conterminous United States (Neilson et al. 1989). Continental-scale transects were constructed through a network of weather stations (Quinlan et al. 1987) to examine the seasonal pattern and spatial extent of homogeneous climatic regions (see methods in Neilson and Wullstein 1983, Neilson et al. 1989). Regional and continental-scale runoff patterns were also examined in this manner using a USGS stream gauge network (US WEST 1988). Average, monthly runoff from watersheds between 100-200 km^2 was normalized by the area of the basin and expressed in millimeters of depth (Neilson et al. 1989). All of the major biotic regions and their ecotones are correlated with major climatic divisions or with the spatial extent of particular types of cold events, such as killing frosts (Ibid.). The timing of rainfall events within each biome promotes the survival of specific life-history types and selects against other life-history types (Neilson 1986, Neilson 1987a).

Two transects delineate most of the potential climatic mechanisms that apparently control the major biomes across the U.S. (after Dice 1943, Küchler 1964, Neilson et al. 1989). For example, the eastern deciduous forest resides in a zone that receives high rainfall throughout the year (Figs. 2, 3). The transition or ecotone with the tall grass prairie occurs where the climate shifts to a summer rainfall peak and a winter rainfall minimum (Fig. 3). The tall grass prairie grades into the short grass prairie coincident with a large drop in summer and winter rainfall (primarily summer). The short grass prairie grades into the sage-scrub of the Great Basin as winter rainfall increases, while summer rainfall decreases even further. The sage-scrub gives way to the west coast forests as winter rainfall increases considerably at the Cascade Mountains. Although summers are generally dry on the west coast, it should be noted

that the Cascades also delimit a large gradient in summer moisture, primarily in the form of humid, marine air (Tibbits 1979).

A transect across the southern tier of States produces a similar array of climatic and biotic zones (Figs. 2, 4). The southeast forest of pines and hardwoods is characterized by high rainfall throughout the year. The southeast forests give way to the southern plains at a regional climatic gradient where both winter and summer rainfall drop to very low values. The southern plains are characterized by spring and fall rains. The spring and fall rains almost cease at the eastern edge of the Sierra Madre Oriental - Rocky Mountain axis (ca. 105° W longitude, Fig. 2). West of this axis are the southwest deserts with spring and fall drought and mid-summer rains (Chihuahuan and Sonoran deserts). The interannual variability of winter rains in the southwest deserts appears to influence the relative dominance of grasslands and semi-desert shrublands in the region (Neilson 1986). The western region of the southwest deserts (the Mohave desert) receives little rain at any time of the year and extends to the coastal mountains. Winter rains again increase on the windward side of the mountains, but not to the amplitude of the Northwest.

The mechanism relating seasonal precipitation patterns to survival of different physiognomic types appears to reside in the regional water balance (Neilson et al. 1989, Stephenson 1990, Woodward 1987). Woody plants appear to rely upon a deep soil reservoir of water to balance the evapotranspiration demand during the growing season. This deep soil reservoir is re-charged each year primarily by winter precipitation. The transition between the eastern forested region and the Great Plains is clearly associated with the seasonality of runoff (Fig. 5, Neilson et al. 1989). The depth of runoff indicates the size of the deep soil reservoir of water. If winter rains are low, woody plants apparently cannot be supported and the abundance of spring and summer rains will determine the extent and biomass of grassland vegetation (Ibid.).

A series of north-south transects, not shown, allow characterizations of the remaining biome-scale ecotones as functions of either rainfall seasonality shifts or physiological thresholds[2] on thermal gradients, often seasonal frost phenomena (Ibid.). The north-south gradients exhibit more cold-temperature constraints than do the east-west gradients. The ecotones are usually defined by some thermal threshold in the physiological processes of plants along these continuous thermal gradients (Burke et al. 1976, Woodward 1987). Although the temperature gradients may not be steep, the ecotone may be sharply defined by virtue of the sharpness of the

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[2]A temperature above or below which plants cannot survive is taken as a physiological threshold.

physiological threshold, such as the latitudinal extent of killing mid-winter frosts. The hardwood forest - boreal forest transition, for example, is controlled by the -40° isotherm, the anucleate freezing point of water (Burke et al. 1976). The ecotone between the eastern deciduous forest and the southeast pines and hardwoods may be controlled by the average extent of hard, winter frosts (Neilson et al. 1989). The ecotones along east-west transects in the conterminous U.S. are primarily related to the amplitude and seasonality of rainfall (Neilson et al. 1989). Thus, all major biome ecotones are associated with well-defined gradients in seasonal weather patterns, or physiological, threshold responses at critical points along thermal gradients.

ECOTONES IN SPACE - LOCAL HABITAT PATTERNS

Each of the broad biomes contain logically arrayed subdivisions (not shown) that reflect topographic, geologic, and land-use patterns. These subdivisions generally capture sub-biome variations in great soil groups, cropping systems, geologic substrate, and other large-scale features (Omernik 1987). These biome subdivisions are, in turn, composed of a mosaic of patches of different quality, arising from variations in soil or micro-topography or successional status (e.g., Whittaker and Levin 1977). Each of these patches can usually be further subdivided on some measurable variability of habitat, and so on. Thus, spatial variability of habitat can usually be described as a hierarchy of different habitat types or qualities on a range of length scales (Allen and Starr 1982, O'Neill et al. 1986). Organisms will tend to 'perceive' a uniform habitat at one or another of these length scales (Neilson and Wullstein 1983). Furthermore, the scaling of habitat by organisms does not appear to occur randomly over a biome. Rather, there appear to be regional gradients in the scaling of habitat variability (Neilson and Wullstein 1983, Peet 1978, Watson 1980). Thus, local community associations appear to be under regional as well as local constraints (Neilson and Wullstein 1983, Ricklefs 1987).

Neilson and Wullstein (1983) described a theory of local habitat size and variability controlled by regional climatic gradients (see also Neilson 1987b). This theory, empirically developed, is quite similar to theories proposed by Stebbins (1952) and Axelrod (1967). In brief, if the regional climate is not overly stressful, organisms do not differentiate subtle

changes in soils, topography or moisture availability[3]. The range of available physical habitats for an organism will fall well within the tolerable physiological limits of the organism. Since minor habitat variability is not 'perceived' by the organism, the diversity of such habitats in the landscape will be comparatively small (Fig. 6). Minor physical differences between microhabitats will still be within the range of physiological tolerance and individuals of the species or of similar species will occupy essentially all microhabitats in the landscape. However, if the regional climate is marginal, minor differences between microhabitats could place some of them outside the range of physiological tolerance, thus, the diversity of 'perceived' microhabitats in the landscape would be higher (Fig. 6). Species diversity increases under these conditions because those microhabitats that are outside the range of tolerance of the 'target' species will be within the range of tolerance of physiologically quite different species, often species from the neighboring biome. Thus, of the variation in geomorphic or edaphic habitats present in the environment, a comparatively larger proportion will be physiologically tolerable in core regions than near ecotones (Neilson and Wullstein 1986). Those contiguous patches of variable substrate that will support a given organism can be grouped into a larger 'homogeneous' habitat patch, accounting for the re-scaling of habitat size along regional gradients. An example will help to clarify these concepts.

Upper elevational boundaries of plant species in the central Rocky Mountains tend to be controlled by cold temperatures (Neilson and Wullstein 1983). This temperature constraint produces a latitudinal gradient in the upper bounds of species ranges (Fig. 7). The lower bounds of species in the central Rocky Mountains tend to be controlled by the amount of growing season rainfall (Ibid.). Since the moisture source is to the south (i.e., the Arizona Monsoon), there exists a latitudinal gradient in the lower bounds of species ranges, opposite in slope to the temperature gradient. The convergence of these two gradients in the northern part of the region constrains the tolerable patches to specific geomorphic facets and soils. That is, usable habitats are small in size and more constrained to particular topographic and soil conditions than further south. Seedling transplant data along local to regional gradients demonstrate the re-scaling

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[3]The concept of regional climatic controls on microhabitat suitability was tested in a transplant study of over 700 tree seedlings (Neilson and Wullstein 1893). Seedlings were planted across gradients of cover, aspect, elevation, and regional climate. Seasonal and year-to-year differences in seedling survivorship were also assessed. Physical measurements of soil moisture through a seasonal drought cycle demonstrated the same principles linking local site suitability and scale to regional climatic stress.

of habitat size as a function of the regional climatic gradients (Ibid.)

Beta diversity, that is, the rate of change of species turnover along a gradient, measured in the southern part of the southern Rocky Mountains should be low compared to that measured further to the north, a result of the regional climatic control of the local suitability of microhabitats. The physical size of a habitable patch in the south is quite large and sweeps over minor variations in substrate and topography where the climate is nearly optimal. However, when the regional environment is stressful, due to drought or other factors, the organisms can survive in only small, select habitats. Thus, patch size will vary or re-scale relative to the organism along regional stress gradients (Neilson and Wullstein 1983, Neilson and Wullstein 1986). Core regions of biomes tend to be less stressful than ecotones, which are, almost by definition, at the limits of tolerance of the organisms on either side.

Is the model of regional control of local habitat size and variability a general model? The single requirement for the model developed in the central Rocky Mountains was that regional temperature and rainfall gradients were not parallel (Neilson and Wullstein 1983). This condition is ubiquitous for the biome ecotones of North America and likely throughout the world (Neilson et al. 1989). Although seasonal temperatures decrease smoothly toward the pole, seasonal rainfall amounts exhibit maxima and minima along any north-south transect. Therefore, at latitudinal ecotones, the temperature and rainfall gradients will not be parallel. Similarly, the east-west transects (Figs. 2, 3 and 4) are remarkable for the variations in rainfall, less so for temperature (data not shown). Again, the two stressors do not produce parallel gradients at any given ecotone. The coincidence of a steep gradient in either rainfall or temperature with known ecotones will be reflected by some form of "wedge" of tolerable environments (as in Fig. 7). Therefore, the pattern of increased beta diversity with proximity to ecotones should be a general phenomenon (Delcourt and Delcourt 1990).

ECOTONES IN TIME - PHYSIOGNOMIC THRESHOLDS

The Whittaker diagram of biome state-space (Fig. 1) is independent of space or time. Temperature or rainfall gradients in space appear to control ecotones between adjacent biomes. However, if the regional climate of a biome were near a physiognomic or ecologic state transition, the entire region could be sensitive to a rapid change of state with a minor change of climate. For example, the recent desertification of the southwest deserts rapidly shifted a large region from semi-desert grassland to desert shrubland with virtually no change in the biome boundaries (Neilson 1986). Similarly, a rapid, regional change from a closed forest to an open savanna

would indicate that a region had passed through a physiognomic threshold (Neilson et al. 1989).

Although the biome diagram (Fig. 1) was constructed for all of the worlds biomes, it is illustrative to plot the positions of several regions of the conterminous U.S. on the diagram to observe their proximity to transition zones in either space or time. This has been done (Fig. 1) for the NE hardwoods, the SE pines, the NW conifers, the SW deserts and the Short Grass and Tall Grass Prairies[4]. Note that the Southwest and Northwest regions plot diagonally from each other.

Several interesting observations emerge. The Tall Grass Prairie region is the only biome that falls well within one of Whittaker's zones, the grassland zone. Recall that this entire area of the diagram indicates a potential transition between grassland and woodland, depending on seasonality and other factors. All other regions plotted on the figure fall on or very near major transition zones. The NW is unique in that it is the only region that is not near a physiognomic transition, that is, it should always be forested. However, it could shift from temperate wet forest to temperate dry forest. Such a shift implies the potential for a large regional expansion of the interior pine forests into the mesic douglas fir forests, a fairly catastrophic ecological and economic change.

The entire eastern forested region could be transitional between temperate forest and temperate woodland, savannah, scrub or grassland, i.e., a major physiognomic change. Such a transition would be consistent with predictions of vegetative changes under global climate change, which indicate possible eastward expansion of grassland and northward shifts of all forest types (Neilson et al. 1989, Winjum and Neilson 1989). It is not clear what vegetation type might dominate the SE. Trees were not supported in forest models under various future climate scenarios for the southern half of the region (Winjum and Neilson 1989). There are, of course, numerous uncertainties with regard to these projections. These include uncertainties in both the General Circulation Models of global climate and the forest succession models. However, these conclusions are supported by an independent analysis (Neilson et al. 1989). If we examine the seasonal runoff patterns in the eastern forests (Fig. 5), it appears that the ubiquitous summer rains over the eastern U.S. are not sufficient to balance the extreme evapotranspiration over the region (Neilson et al. 1989). Streams in the region are drawn down by regional evapotranspiration to a

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[4]Regional ranges of annual temperature and rainfall were visually extracted from National contour maps of climate (USDA 1941) using the regional boundaries from Figure 2 and plotted on the Whittaker diagram (Fig. 1).

minimum flow in the summer when rainfall is still quite high (Ibid.). The trees are apparently reliant upon a deep soil reservoir of water that is recharged by winter rains. If either the winter rains decline or the summer transpiration increases due to increased temperatures, large regions of the country could experience summer soil moisture deficits. Such moisture deficits could trigger the kind of physiognomic transition implied by the Whittaker biome diagram (Fig. 1).

The Short grass prairie and the SW deserts receive similar amounts of rainfall and are both transitional between grassland and desert physiognomies (Fig. 1). Yet, the prairie appears to be more resilient as a grassland with few desert species, while the deserts are floristically more representative of true deserts. A regional and rapid transition from semi-desert grassland to desert shrubland in the southwest has already been observed and attributed to a combination of overgrazing and climatic variation (Neilson 1986). During the dustbowl of the thirties, the short grass prairie also clearly desertified with a cessation of spring rains (Neilson et al. 1989). However, unlike the Southwest, the prairie region has returned to a grassland condition with the return of spring rains. It is interesting that the SW desertification shows little signs of rebounding to grassland even with the amelioration of overgrazing. The lack of recovery may be due to the regional lack of the spring rains which appear to be important in favoring the physiognomy of grasslands (Neilson 1987a) and to significant changes in soil structure and fertility (Whitford et al. 1987). The differences between the two semi-arid regions could be due to their different patterns of rainfall seasonality, wet springs in the prairie and dry springs in the desert (Neilson 1987a, Neilson et al. 1989).

Thus, there could be thresholds of ecological change that pertain to entire regions. Spatial ecotones at the biome scale appear to be primarily controlled by rather sharp changes in seasonal climatic regimes or the spatial location of physiological temperature thresholds. In contrast, within biome, rapid temporal changes (thresholds) could be manifested as regional changes in the amplitudes of seasonal weather patterns (as distinct from changes in seasonality). For example, an increase in summer temperature and potential evapotranspiration could fully deplete a deep soil reservoir of water producing a threshold change in the physiognomy of a forested region with no change in regional rainfall patterns.

Ecotones that are constrained by winter or spring cold events could, in response to climatic change, tend to shift rapidly along shallow latitudinal temperature gradients. These rapid changes would be constrained by the lags in response of the biota (Neilson et al. 1989, Winjum and Neilson 1989, Woodward 1987). Thus, some biomes could undergo rapid changes in their boundaries as well as regional, threshold changes in physiognomy. Within

biome changes are likely a combination of spatial shifts of edges of homogeneous climatic regions and within biome (climatic region) changes in seasonal amplitudes. If climatic change were to force some of these regional biomes toward thresholds of change, how fast would the change occur? What would be the nature of the changes, and would there be early warning signs?

CLIMATIC CHANGE - ECOTONES AND THRESHOLDS

The rate of global climatic change anticipated within the next century could be extreme enough to essentially uncouple some ecosystem components from the climate system. For example, the southeast forests could be subjected to severe summer drought, and therefore cease reproduction and undergo widespread decline (Winjum and Neilson 1989). The climate, primarily the thermal regime, of the forests throughout the eastern U.S. could shift on the order of 500-1000 km to the north within a hundred years due to global warming (Ibid.). However, most heavy seeded trees can only migrate about 10-40 km per century (Zabinski and Davis 1989). Furthermore, it usually requires several decades for a tree to reach reproductive age. If we were to plant tree seedlings to the north in regions that we expect to be favorable as adults, they would likely not survive today's climate. If we plant seedlings in northern reaches that will survive today's climate, they might not be well adapted to the climate as mature individuals. In this case the disturbance is chronic, yet not from any particular stress of climate, rather from the rate of change of climate. Organisms with short life-cycles would be favored. As they reproduce and die, the climate continues to change and different species would colonize. The community (composed of short-lived organisms in any one location) might be constantly changing, but might be considered to be in equilibrium with the present, changing climate. In effect, the communities could be relegated to a semi-permanent early successional status. With a drying of the summers, the forests of the southeast, could shift to a mediterranean (i.e., dry summer) hydrology, with possibly a savanna to woodland or some other arid component. All of the forested regions of the U.S. are potentially susceptible to similar, widespread physiognomic change.

Over geologic time large-scale biogeographic changes typically occurred in a quasi-equilibrium sense for all organisms, not just those with short life-cycles. That may not be the case in the future. The rate-of-change disturbance represents a partial uncoupling of the spatial and temporal response characteristics of the climate from the response characteristics of many extant species. That is, normally slow changes over large areas could become fast changes over large areas.

Most of the regional ecological impacts from global climatic change

could result from changes in the regional water balance, largely induced by increased potential evapotranspiration. These conclusions carry the assumption that the direct effects of elevated CO_2 concentration will have little to no affect on plant water use efficiency (WUE) at landscape scales. This is somewhat distinct from potential increases in WUE at the level of the leaf, when stomata are open. However, if increased WUE were to actually have an impact on regional water balance, biomes might become more drought tolerant. The widespread negative effects might not occur (Neilson et al. 1989). The direct effects of elevated CO_2 represent significant uncertainties in projecting the potential impacts of climatic change on biomes.

MONITORING TO DETECT CHANGE - ECOTONES AND THRESHOLDS

How would we monitor for impending changes such as those described? What would we measure to determine a spatial shift in an ecotone or to determine the proximity to a physiognomic threshold in time. Annual climatic statistics could in many cases be quite useful in signaling proximity to an ecological threshold (Fig. 1). However, changes in the seasonality will provide greater accuracy in locating climatic gradients associated with ecotones. Tracking movements of climatic gradients through space will be important. But, monitoring the response of the vegetation will be more challenging.

The size distribution of habitats as 'perceived' by plants appears to shift to smaller, more diverse patches as one moves toward an ecotone. Habitat size and variability can be measured along regional transects to determine the spatial location of the actual transition zone (Neilson and Wullstein 1983). The same phenomenon should occur through time, that is, the 'perceived' size distributions of habitats should shift to smaller, more diverse patches as a region shifts toward an ecological threshold (Ibid.).

The potential impacts of climatic change on habitat size and variability can be easily demonstrated with a thought experiment. A hilly region, normally dry, is slowly flooded by water. The initial, homogeneous patch (from the plant 'perspective') is one of all dry land. As the water level rises, the valley bottoms would produce a distribution of small wet patches in a dry matrix. As the water rises further, the small patches merge into fewer, large and homogeneous patches. At some point these will merge into a matrix and the dry land will become isolated into ever smaller sized patches. That is, the wet-island, dry-matrix pattern reverses to a wet-matrix, dry-island pattern. Computer experiments indicate that such patterns of habitat fragmentation produce thresholds in regional ecological processes, e.g., seed dispersal or the spread and magnitude of disturbance (Gardner et al. 1987, Turner et al. 1988, Turner et al. 1989). That is, a

critical level of habitat fragmentation will produce or release barriers to many horizontal processes of movement. Thresholds that alter the horizontal spread or movement of energy and material are distinct from the physiognomic threshold discussed earlier. Thus, there exist two different kinds of thresholds that could be approached as a region is subjected to climatic change, 1) physiognomic change, and 2) truncation or release of horizontal landscape processes.

History can also impart pattern to patch structure at spatial bounds. Another example will be illustrative. Begin with the same thought experiment, only impart an incline to the water table before it rises throughout the region. As the water table rises, valley bottoms on one end of the region would start to fill before those at the other end, producing a well-defined 'migrational' front of wet patches. Even though there may be valleys at the other side of the region that are lower in elevation, they will not be initially occupied by water. Similarly, the migrating front of a species' distribution tends to be sharply defined, while the trailing edge is fuzzy as it leaves behind isolated relics. As we approach temporal thresholds, there should also be predictable patterns of response by the invading versus the declining species. Such changes in patch size distribution over a whole region could be measured both remotely and from the ground. A bioassay of habitat size and variability is one approach to this measurement (Neilson and Wullstein 1983). Physical measurements of soil moisture through time can also indicate directional changes in patterns of habitat size and variability as regional conditions become more stressful (Ibid.). These characteristics could potentially be measured remotely and calibrated to ground data.

CONCLUSIONS

In summary, regional ecological change, induced by climatic change, could be manifested in at least two ways: 1) changes in the boundaries of regions and 2) rapid changes in the qualities within regions. The hypothesis is presented that the concept of ecotones is equally applicable to both types of change. Ecotones in space are considered in the classical context as spatial discontinuities separating distinct ecological communities at any spatial scale, from biomes to interpatch differences. Ecotones in time are defined as ecological or physiognomic thresholds that exist throughout a region or biome and would become manifest as rapid transitions from one biotic community to another under relatively minor changes in climate.

Transitions in community composition could be significant physiognomic transitions and might be facilitated by a catastrophic shift in the regional disturbance regime. That is, if a forest, for example, were forced by

drought stress from a closed forest condition to an open savanna, the change would likely be mediated by regional increases in disease and wildfires. As the landscape proceeds through a rapid change in habitat size and variability, thresholds in the horizontal movement of seeds, pollen and wildlife, and the spread of disturbance would likely be encountered. The potential magnitude of the spatial changes in ecotones is on the order of several hundred kilometers of horizontal movement and up to a thousand meters of vertical rise in a few decades (Neilson et al. 1989, Winjum and Neilson 1989). Such rapid changes in habitat patterns could produce the extinction of many species.

Although climatic change could, by itself, alter ecotone locations and regional ecosystem physiognomy, secondary influences such as disturbance regimes would likely modulate the location of the boundary or the timing and magnitude of the regional physiognomic change. For example, fires in a prairie could burn into an adjacent forested region shifting the ecotone from its climatically preferred position. Likewise, if a landscape is favored by climatic change to shift from a closed forest to an open savanna, a large, regional wildfire could produce a physiognomic overshoot. That is, as the forest drys out, there should be a natural reduction in the leaf area, toward the savanna condition. However, the fuel load could result in a large fire that might clear the landscape. The re-establishment of trees, even at a lower density could take some time, or with continuing climatic change, might not occur. Thus, the disturbance could induce a landscape change from a closed forest directly to an open grassland or shrubland, bypassing the climatically preferred savanna.

A regional monitoring program should be structured as an early warning system of such regional threshold changes. The system should be based in remote sensing to provide a regional perspective, but should be calibrated to measurable, local-scale patterns. The concept of regional control of local habitat patch size is presented as providing a potential signature of proximity to an ecotone, either in space or time and the temporal dynamics of that ecotone. Patches are hypothesized to be large in core regions and small and diverse near transition zones. To determine the scale of habitat patches and detect changes in that scale along regional and temporal gradients, monitoring programs will require careful design. Managers should address these design considerations in current planning efforts. They should also consider the prospect of regional ecological thresholds and the impacts of different management practices when confronting rapid change, increased disturbance regimes, new species mixes and altered landscape patterns. Careful management of disturbance regimes through manipulations of fuel load or cutting practices, for example, will be important in minimizing both the magnitude of ecological changes and the rate of the

changes over regional extents. A combination of purely observational data and bioassay approaches should be considered when monitoring for ecological change. Monitoring indicators should be developed to provide useful information at a range of scales from individual organism responses to landscape patterns.

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FIGURE LEGENDS

Figure 1. Plot of world biome types as a function of mean annual temperature and rainfall. The grassland area is broadly transitional and could be either grassland or some form of open woodland or scrub depending on other factors, such as climate seasonality, soils or disturbance. The transitions between biomes as indicated by dividing lines are also approximate, depending on a similar set of other factors (after Whittaker 1975).

Figure 2. Biomes of the United States (modified from Dice 1943, and Küchler 1964). The climatic transects are shown (Figs. 3, 4). The hydrologic transect (Fig. 5) closely follows the northern climatic transect.

Figure 3. Seasonality of mean total monthly precipitation across the United States along the northern transect (Fig. 2). a) The vertical axis represents precipitation (mm/month), the horizontal axis represents months of the year, and the diagonal axis represents longitude. The locations of the weather stations used to construct the graph are indicated by horizontal lines. Total monthly precipitation data from 1941-1970 were used to calculate the mean values depicted here (Quinlan et al. 1987). b) Contour map of the three dimensional surface. The contour interval is 10 mm. Solid lines to the right of the contour plot indicate the positions of ecotones along the transect, as taken from Fig. 2. CV - California Vegetation, PNW - Pacific Northwest Forests, GBS - Great Basin Sagebrush-Steppe, GBD - Great Basin Desert Scrub, NRM - Northern Rocky Mountain Forests, SRM - Southern Rocky Mountain Forests, SWD - Southwestern Deserts, SGP - Short Grass Prairie, TGP - Tall Grass Prairie, STS - South Texas Savanna, NH - Northern Hardwoods, EDF - Eastern Deciduous Forests, SEF - Southeastern Forests. c) The elevations (m) of the weather stations and of the stream gauging stations (Fig. 5).

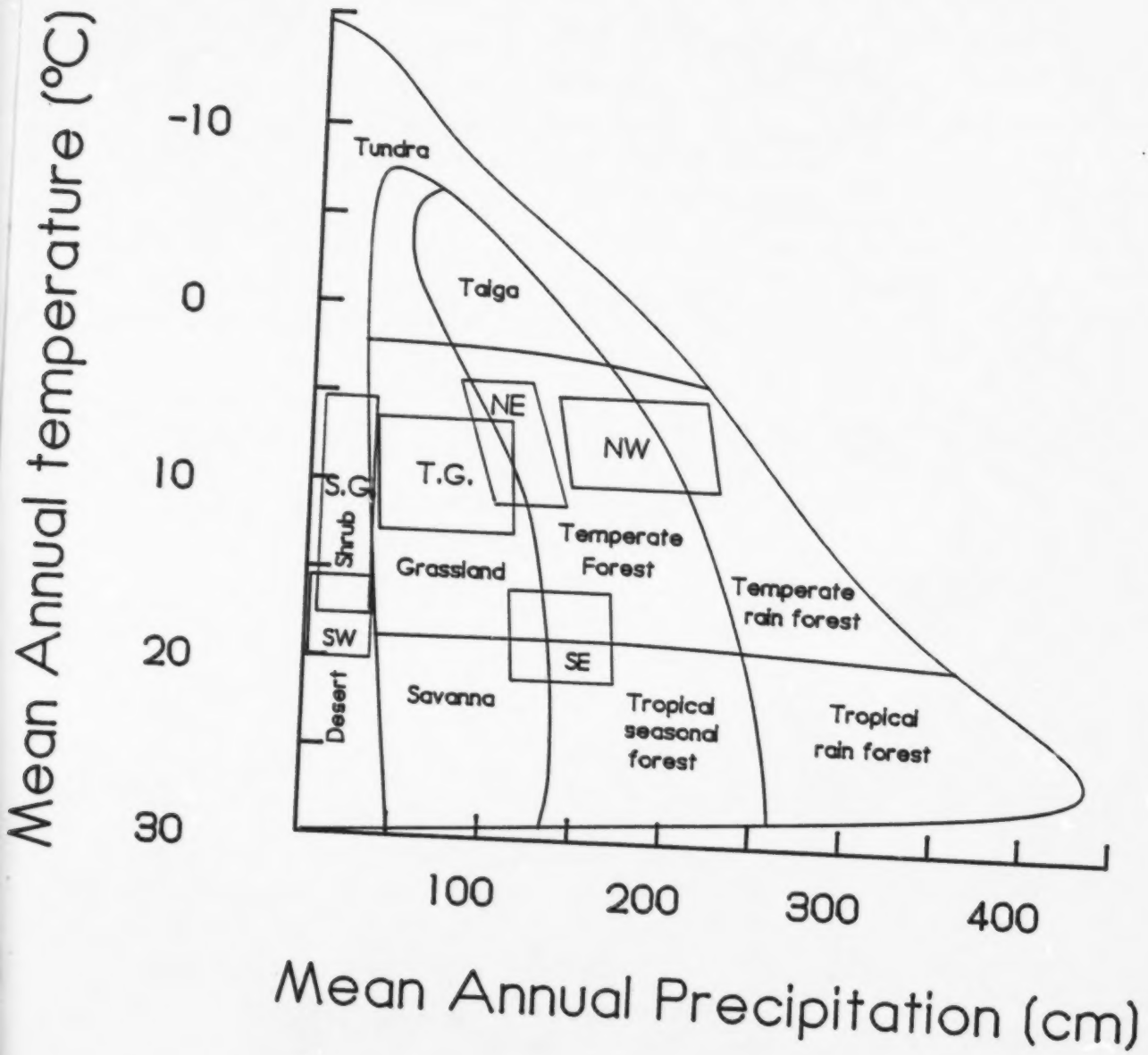
Figure 4. Seasonality of precipitation across the southern transect. Legends a), b) and c) are as in Fig. 3.

Figure 5. Seasonality of monthly runoff across the United States along the northern transect (Figs. 2, 3). a) The vertical axis represents equivalent depth (mm), the horizontal axis represents months of the year, and the diagonal axis represents longitude. The location of the gauging stations used to construct the graph are indicated by horizontal lines. At least 15 years of data were used to calculate the mean values (US West 1988). b) Contour map of the three dimensional

surface. The contour interval is 5 mm. Solid lines to the right of the contour plot indicate the positions of ecotones along the transect, as taken from Fig. 2. See Fig. 3 for key to abbreviations. The elevations (m) of the gauging stations are shown in Fig. 3.

Figure 6. The hypothetical diversity of habitats along a transect stretching from one biome to another, across a major ecotone.

Figure 7. A conceptual model of the regional climatic constraints on the vertical distribution and composition of plant communities along a regional climatic gradient (after Neilson and Wullstein 1983, Neilson 1987b). As the gradients converge at the apex of the 'wedge', the size of suitable habitat patches decreases, while their diversity increases (see Fig. 6).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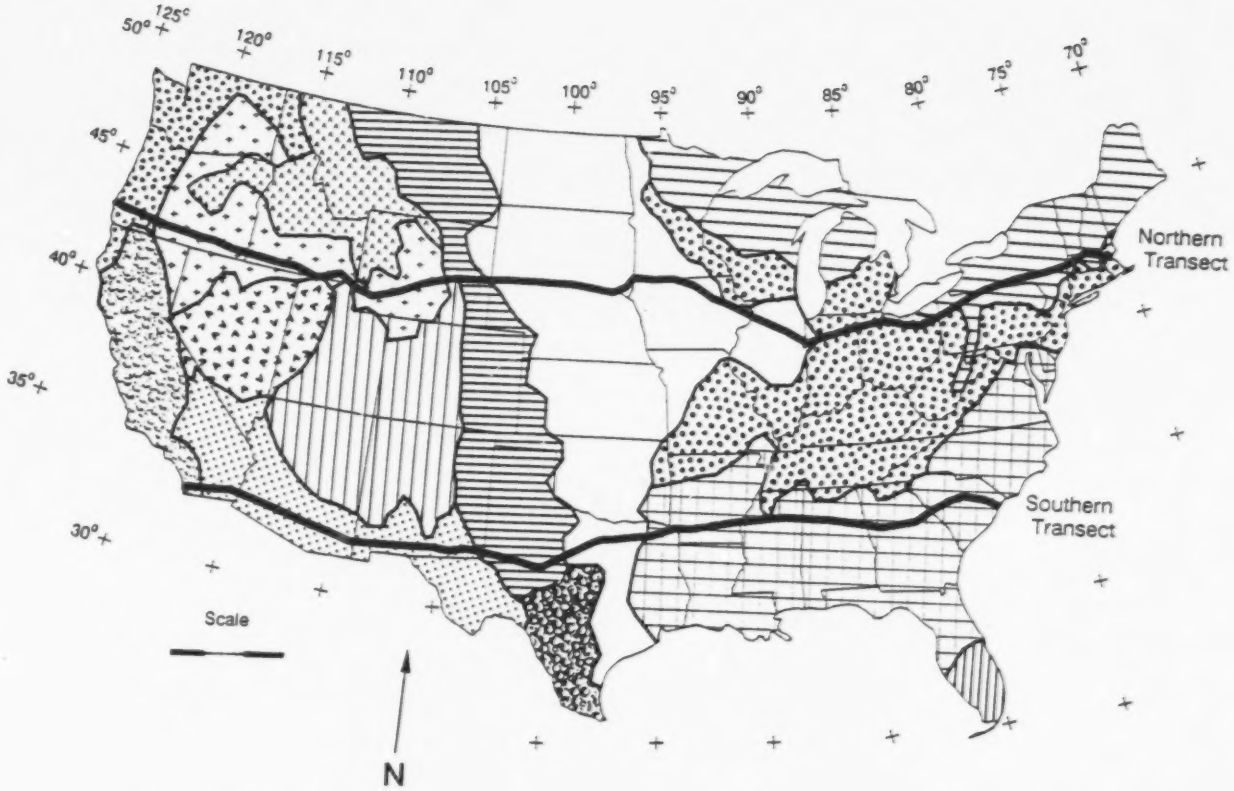
20
30
Tundra
Taiga
NE
NW
T.G.
S.G.
Shrub
Grassland
Temperate Forest
Temperate rain forest
SW
SE
Desert
Savanna
Tropical seasonal forest
Tropical rain forest
100
200
300
400
Mean Annual Precipitation (cm)

Figura 1



Biotic Regions

- California Vegetation
- PNW Forests
- Great Basin Sage-Steppe
- Great Basin Desert Scrub
- Northern Rocky Mountain Forests
- Southern Rocky Mountain Forests
- Southwestern Deserts
- Short Grass Prairie
- Tall Grass Prairie
- South Texas Savanna
- Northern Hardwoods
- Eastern Deciduous Forests
- Southeastern Forests
- Subtropical Forests

Figure 2

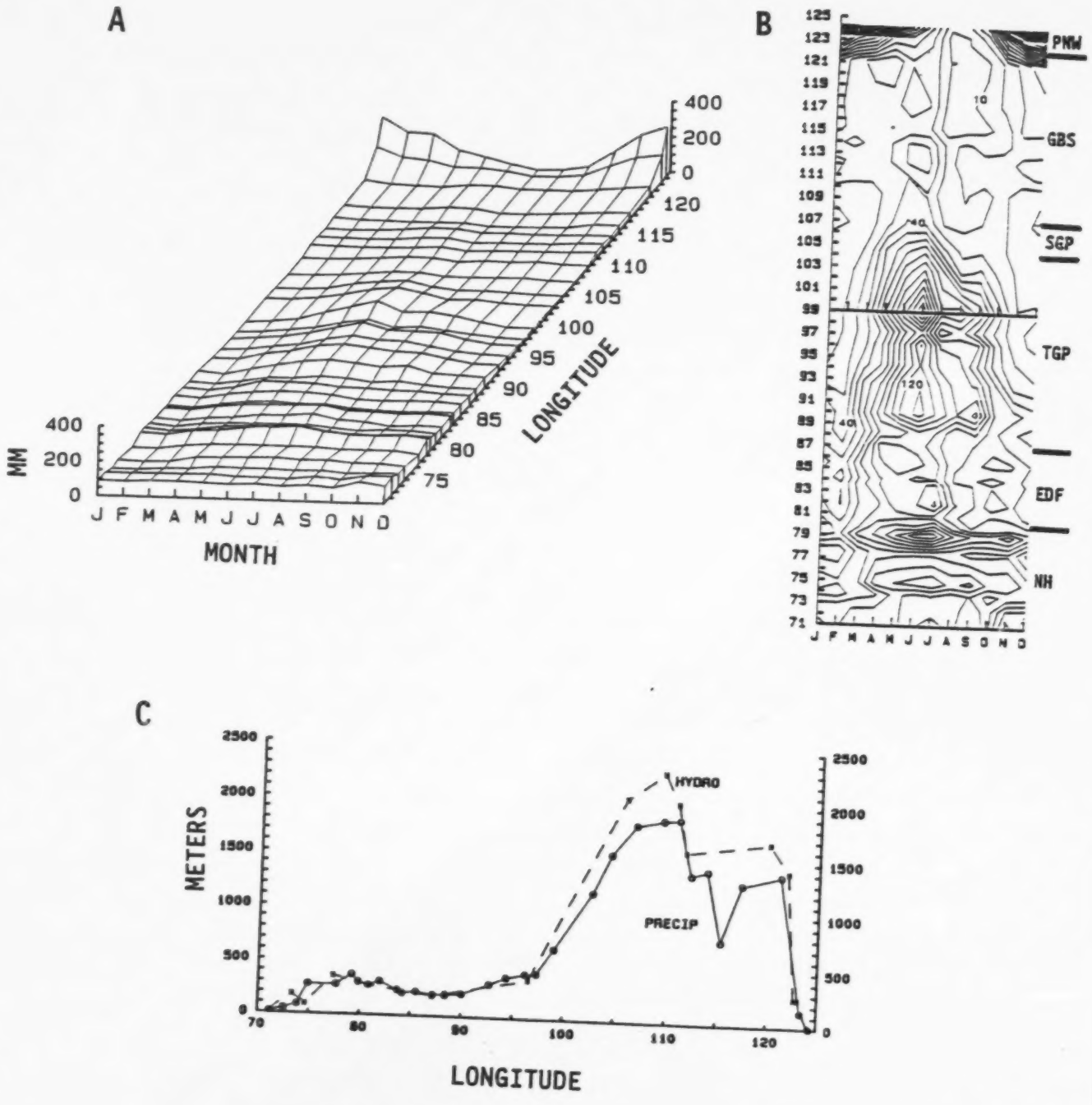

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Figure 3

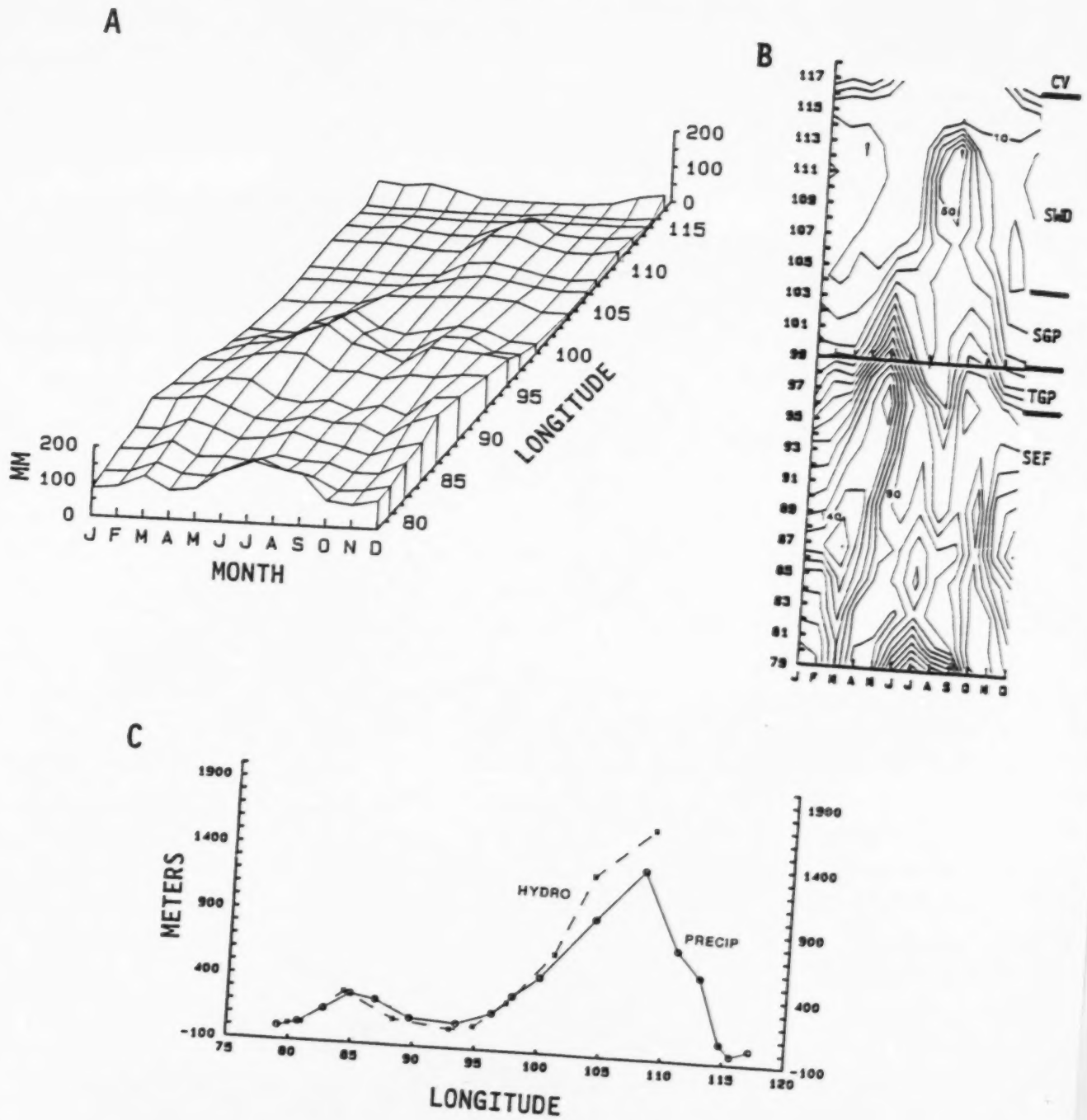
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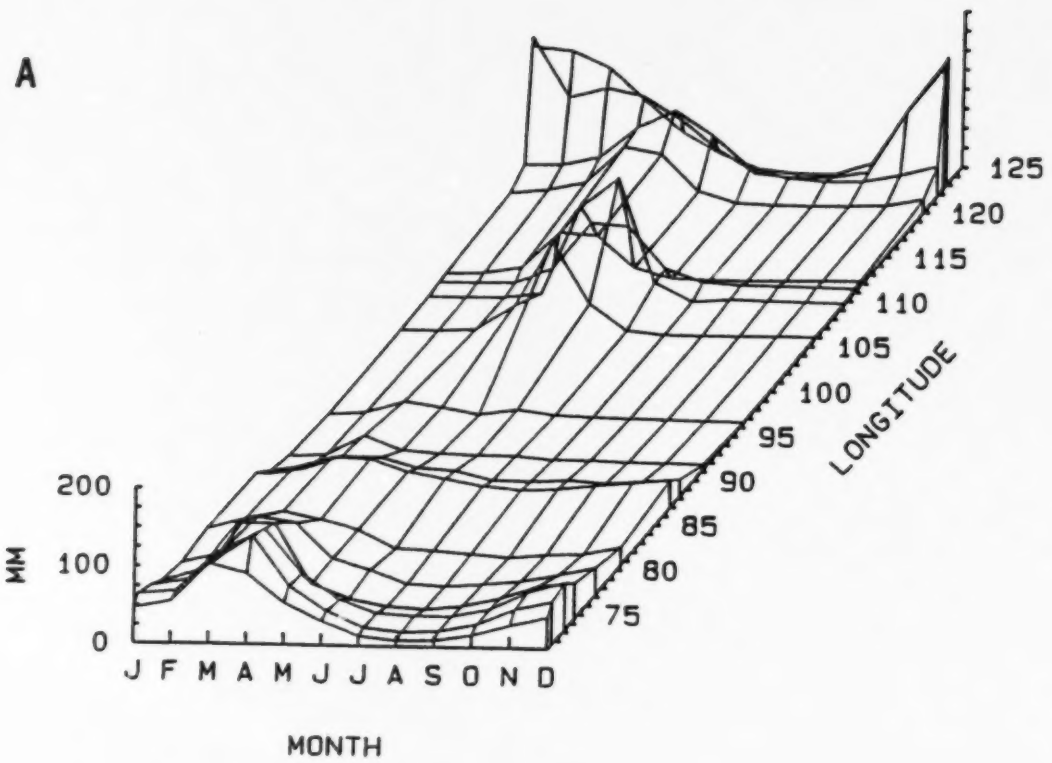
Figure 4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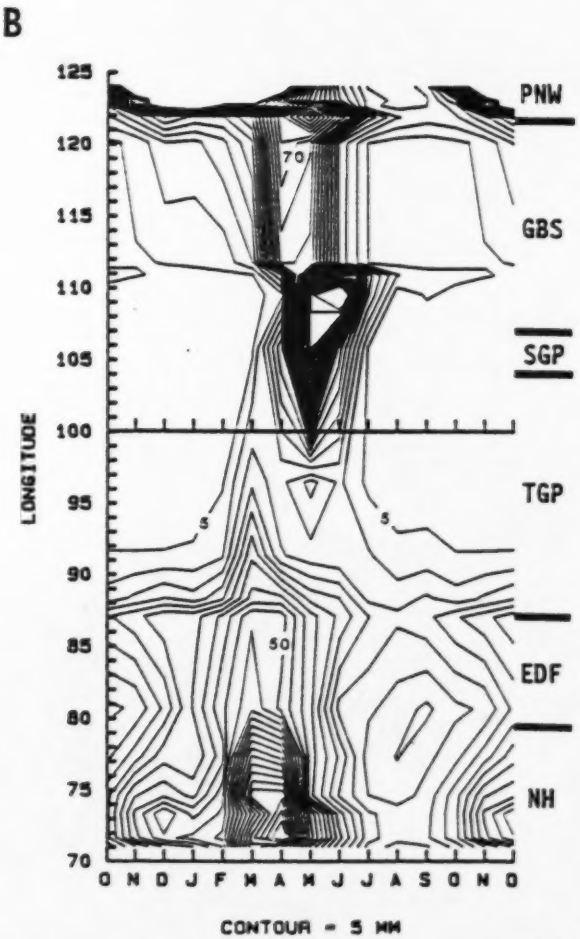
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Figure 5

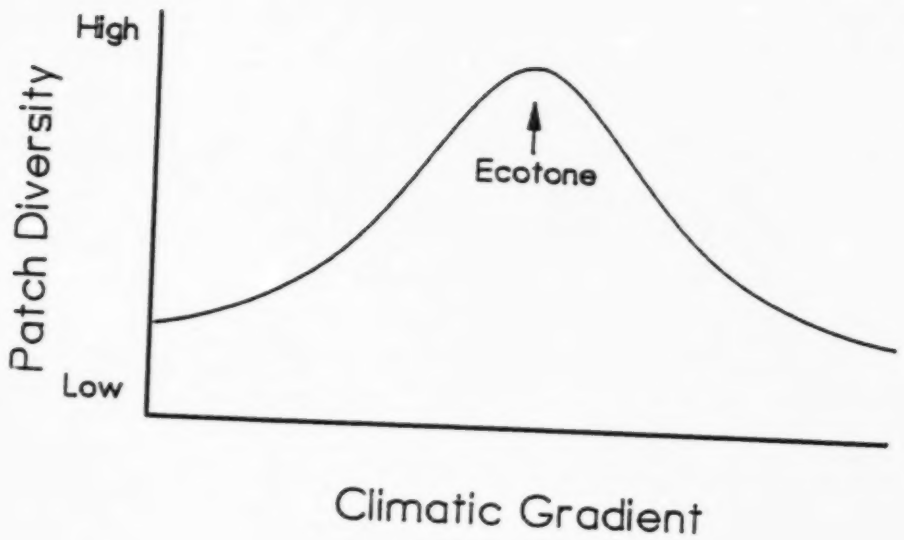

Figure 6

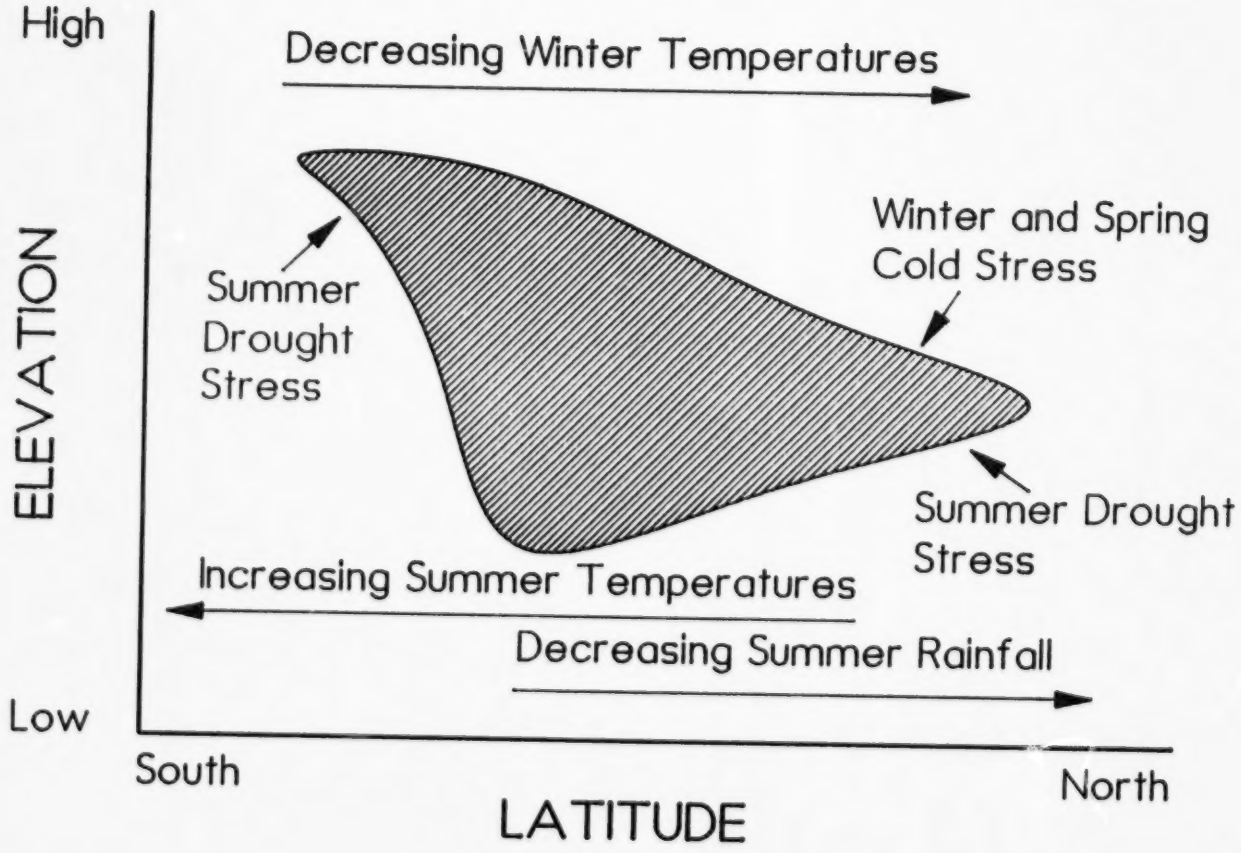
High
Decreasing Winter Temperatures
ELEVATION
Summer
Drought
Stress
Winter and Spring
Cold Stress
Summer Drought
Stress
Increasing Summer Temperatures
Decreasing Summer Rainfall
Low
South
North
LATITUDE

Figure 7